

Nutrient Vectors and Riparian Processing: A Review with Special Reference to African Semiarid Savanna Ecosystems

S. M. Jacobs,^{1,9,*} J. S. Bechtold,¹ H. C. Biggs,² N. B. Grimm,³ S. Lorentz,⁴ M. E. McClain,⁵ R. J. Naiman,¹ S. S. Perakis,⁶ G. Pinay,^{7,10} and M. C. Scholes⁸

¹School of Aquatic and Fishery Sciences, University of Washington, Campus Box 355020, Seattle, Washington 98195-5020, USA; ²Scientific Services, Kruger National Park, Private Bag X402, Skukuza, 1350, South Africa; ³School of Life Sciences, Arizona State University, Tempe, Arizona 85287-4501, USA; ⁴School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa; ⁵Department of Environmental Studies, Florida International University, Miami, Florida 33199, USA; ⁶USGS Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon 97331, USA; ⁷Centre d'Ecologie Fonctionnelle & Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France; ⁸School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS, 2050, South Africa; ⁹Department of Conservation Ecology and Entomology, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa; ¹⁰University of Birmingham, GEES, Edgbaston, Birmingham, B15 2TT, UK

ABSTRACT

This review article describes vectors for nitrogen and phosphorus delivery to riparian zones in semiarid African savannas, the processing of nutrients in the riparian zone and the effect of disturbance on these processes. Semiarid savannas exhibit sharp seasonality, complex hillslope hydrology and high spatial heterogeneity, all of which ultimately impact nutrient fluxes between riparian, upland and aquatic environments. Our review shows that strong environmental drivers such as fire and herbivory enhance nitrogen, phosphorus and sediment transport to lower slope positions by shaping vegetative patterns. These vectors differ significantly from other arid and semiarid ecosystems, and from mesic ecosystems where the impact of fire and herbivory are less pronounced and less predictable. Also unique is the presence of sodic soils in certain hillslopes, which substantially alters hydrological flowpaths and may act as a trap where nitrogen is immobilized while sediment and phosphorus transport is enhanced.

Nutrients and sediments are also deposited in the riparian zone during seasonal, intermittent floods while, during the dry season, subsurface movement of water from the stream into riparian soils and vegetation further enrich riparian zones with nutrients. As is found in mesic ecosystems, nutrients are immobilized in semiarid riparian corridors through microbial and plant uptake, whereas dissimilatory processes such as denitrification may be important where labile nitrogen and carbon are in adequate supply and physical conditions are suitable—such as in seeps, wallows created by animals, ephemeral wetlands and stream edges. Interaction between temporal hydrologic connectivity and spatial heterogeneity are disrupted by disturbances such as large floods and extended droughts, which may convert certain riparian patches from sinks to sources for nitrogen and phosphorus. In the face of increasing anthropogenic pressure, the scientific challenges are to provide a basic understanding of riparian biogeochemistry in semiarid African savannas to adequately address the temporal and spatial impact of disturbances, and to apply this knowledge to better regional land and water management. An

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*Corresponding author; e-mail: sjacobs@sun.ac.za

integrated, multidisciplinary approach applied in protected as well as human-disturbed ecosystems in southern Africa is essential for underpinning a strong environmental basis for sustainable human-related expansion.

INTRODUCTION

Riparian zones are increasingly valued as sinks for anthropogenically derived nutrients, thus protecting fluvial ecosystems against elevated nitrogen and phosphorus loads, and ultimately eutrophication (Fenn and others 1998; Smith and others 1999; Naiman and others 2005b). Lying at the interface between terrestrial and aquatic ecosystems, riparian zones collect surface and subsurface runoff moving from uplands to adjoining aquatic ecosystems (Naiman and Décamps 1997; Fisher and others 2004). Water containing nitrogen and phosphorus is also transported longitudinally from upstream and much can be filtered laterally through riparian sediments. This hydrologic connectivity, along with unique soil physical and redox conditions and elevated phytomass in the riparian zone, allows for the retention of nitrogen and phosphorus and the protection of downstream, recipient waters (lakes, reservoirs, and coastal ecosystems) from eutrophication and sedimentation (Naiman and Décamps 1997; Fisher and others 2004; Belnap and others 2005).

Much of our current understanding of catchment and riparian biogeochemistry and linkages between terrestrial and aquatic ecosystems has been obtained through studies carried out in afforested and agricultural humid-temperate regions (Jacobs and Gilliam 1985; Peterjohn and Correll 1984; Cirimo and McDonnell 1997; Caraco and Cole 2001), with a smaller pool of knowledge on well studied arid ecosystems such as Sycamore Creek, Arizona (for example, Grimm 1987; Grimm and Petrone 1997; Schade and others 2002). Comparatively little research has been carried out in savannas, especially those in semiarid and arid regions, even as population growth and associated landuse change are rapidly accelerating (Jackson and others 2001; Pollard and others 2003; Venter and others 2007). Savannas are characterized structurally by the co-dominance of trees and grasses and climatically by distinct dry and wet seasons, with most of the annual precipitation concentrated in a discrete wet season (Skarpe 1992; Scholes and Walker 1993; Venter and others 2003). Nutrient transformations and fluxes are closely linked to rainfall, with large pulses in biological activity following precipitation

Key words: riparian biogeochemistry; nitrogen; phosphorus; semiarid landscapes; fluvial disturbance; South Africa.

events, especially those occurring after long dry spells (Noy-Meir 1973; Austin and others 2004). In near-pristine semiarid savannas herbivores and fires act as strong drivers on ecosystem processes (Frost and Robertson 1987; du Toit and others 2003), although the influence of these vectors on nutrient redistribution has received little attention. Large infrequent disturbances such as floods and fires in riparian areas alter heterogeneity and rearrange patches at several scales (van Collier and others 2000; Parson and others 2005; Pettit and Naiman 2005). The pulsed nature of most ecosystem processes, complex hill slope hydrology, inherent heterogeneity and disturbance regimes in semiarid ecosystems contrasts somewhat with mesic ecosystems (for example, Cirimo and McDonnell 1997; Décamps and others 2004; Naiman and others 2005a) and impacts hydrologic connectivity, water residence time and biogeochemical dynamics in savanna riparian zones.

Understanding upland-riparian-riverine linkages has become paramount as the savannas of southern Africa are rapidly transformed to sustain economic development and population growth (Pollard and others 2003; Venter and others 2007). In this review article we focus on perennial rivers transecting semiarid savannas and examine the vectors of nitrogen and phosphorus transport, nutrient transformations, and the effects of disturbances on biogeochemical linkages between uplands, riparian zones and rivers. We examine vectors of nutrient delivery to the riparian zone, processing of nutrients in riparian soils and vegetation, and the effect of disturbance on riparian biogeochemistry. We also contrast riparian biogeochemistry in semiarid savannas, such as the Lowveld savanna in South Africa (Kruger National Park), with examples from other semiarid (Sonoran Desert) as well as temperate ecosystems (Yellowstone National Park), where fundamental differences exist.

LATERAL DELIVERY OF NUTRIENTS

Nitrogen and phosphorus in the soil are transferred from terrestrial to fluvial environments as dissolved or particulate forms in overland flow or as dissolved forms in subsurface flow (Schlesinger and others 1999; Belnap and others 2005; Figure 1). However,

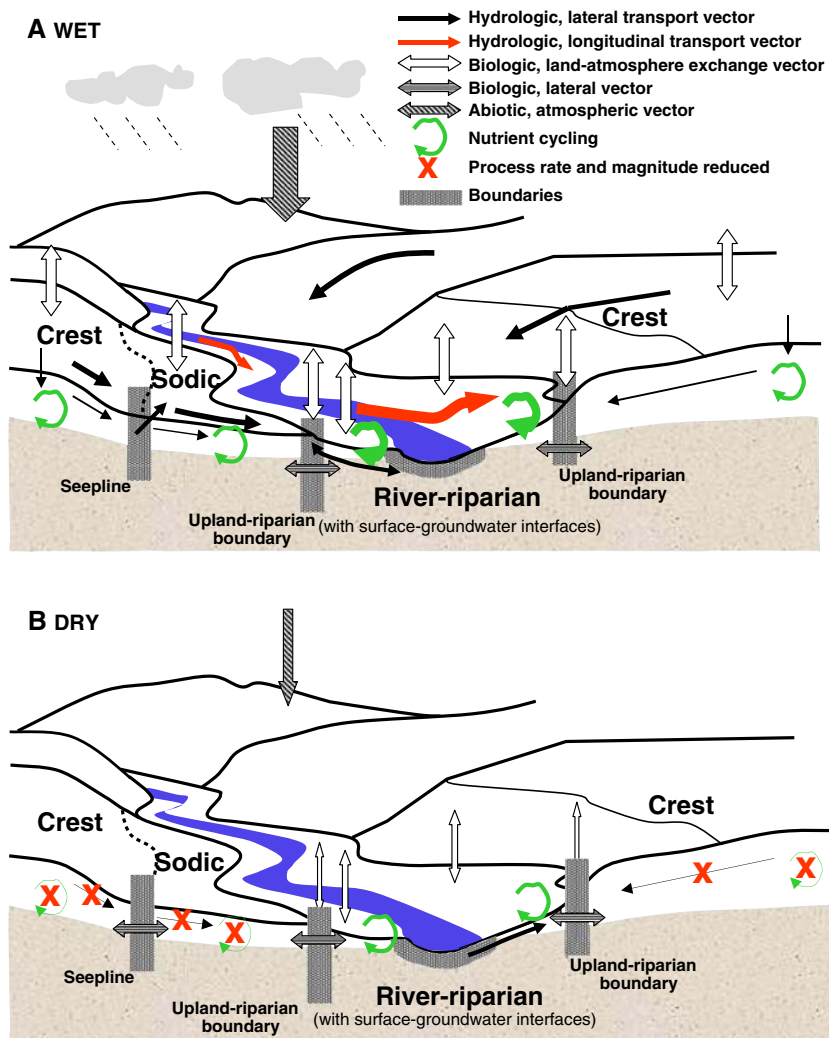


Figure 1. Routes for delivery and processing of nitrogen and phosphorus to semiarid riparian zones during wet and dry seasons. Relative size of arrows indicates the magnitude of transfer of nutrients to the riparian zone (generally nitrogen > phosphorus). Nitrogen and phosphorus can be delivered vertically through an atmospheric vector, laterally through biologic and hydrologic terrestrial vectors and laterally through a hydrologic fluvial vector. Processing can take place at the boundaries between patches, or within patches. In semiarid savannas distinct wet (*top*) and dry (*bottom*) seasons are encountered, and transport and processing are accordingly affected. For example, lateral biologic vectors may be particularly important in transferring nutrients during dry periods in African savannas, when ungulate herbivores congregate along watercourses.

fundamental differences exist in the major vectors for nitrogen and phosphorus in savannas; fire and biogenic emissions are dominant vectors for nitrogen output whereas sediment transport is the major pathway for phosphorus redistribution, along with significant quantities of nitrogen in soil solution (Schlesinger and others 2000; Fierer and Gabet 2002; Scholes and others 2003; Welter and others 2005). Leaching (downward movement of water below the root zone) into groundwater flow is an additional pathway by which nutrients are delivered to riparian environments but is more important in mesic than in semiarid and arid ecosystems (Seyfried and others 2005). In each case, it is the ecological patterns and processes in savanna uplands that impart a unique signature to the lateral delivery of nutrients (and sediments) to riparian areas.

Nutrient Cycling in Savanna Uplands

Semiarid and arid ecosystems generally contain smaller nitrogen and phosphorus stocks and exhibit

lower available nitrogen and phosphorus concentrations than many mesic ecosystems; this is also evident for savanna (Scholes and others 2003; Table 1). Mechanisms such as internal re-translocation and storage in savanna vegetation (Tolsma and others 1987), and soil microbial and abiotic immobilization in rangelands (Kellman and Sanmugadas 1985; Kellman and others 1985; Barrett and Burke 2000; Barrett and others 2002) reduce leaching of inorganic nitrogen and phosphorus from surface soils to deeper soil horizons and may thereby reduce delivery to riparian areas and streams. Large herbivores, ubiquitous in protected African savanna, are thought to promote conservation of nutrients near the soil surface, thus further reducing nutrient leaching (McNaughton and Coughenour 1981; Skarpe 1992). In addition, horizontal vectors of nutrient loss are, in general, more important in semiarid and arid than in mesic environments but are restricted to wet periods (Fisher and others 2004; Welter and others 2005; Figure 1).

Table 1. A Comparison of Biophysical and Biogeochemical Parameters between examples of Semiarid African, Semiarid North American and Temperate North American Ecosystems

	African semiarid tropical ecosystem (Kruger National Park, South Africa)	North American temperate semiarid ecosystem (Sonoran desert, USA)	North American temperate ecosystem (Yellowstone National Park, USA)
Mean annual temperature (°C)	21–23 (1)	20 (2)	2–7 (3)
Mean annual precipitation (mm)	405–547 (1)	390–510 (4)	400–750 (5)
Nitrogen deposition (kg N ha ⁻¹ y ⁻¹)	21.6 (6)	0.7–1.1 (7)	<2.5 (nitrate) (8)
Nitrogen stocks (kg N ha ⁻¹)	3,060–4,635 (6)	1,600 (9)	3,510–37,050 (10)
Nitrogen mineralization—uplands (µg N g ⁻¹ soil day ⁻¹)	–0.15–0.24 (6) ¹⁷ –0.40–0.30 (11) ¹⁷	0.05–0.3 (12) ¹⁷	0–0.35 (13) ¹⁷
Nitrogen mineralization—sodic zone (µg N g ⁻¹ soil day ⁻¹)	0.0–0.5 (11) ¹⁷	Not comparable	Not comparable
Nitrogen mineralization—riparian wetlands (µg N g ⁻¹ soil day ⁻¹)	–0.60–0.45 (11) ¹⁷	0.3–0.85 (12) ¹⁷	0–1.40 (3) ¹⁷
Denitrification enzyme activity (water, glucose, nitrate amended)—uplands (µg N (N ₂ O) kg ⁻¹ h ⁻¹)	0.0–0.5 (11)	1.3–8.2 (13)	4–63 (3)
Denitrification enzyme activity (water, glucose, nitrate amended)—sodic zone (µg N (N ₂ O) kg ⁻¹ h ⁻¹)	2.0–10.0 (11)	Not comparable	Not comparable
Denitrification enzyme activity (water, glucose, nitrate amended)—riparian wetlands (µg N (N ₂ O) kg ⁻¹ h ⁻¹)	4.0–33.0 (11)	58–80 (14)	281–583 (3)
Fire frequency in uplands (years)	4.3–9.1 (15)	Data not available	20–25 (15)
Herbivore biomass (kg ha ⁻¹)	32–37 (16)	Data not available	37 (5)

(1) Venter and others (2003), (2) Balling and others (1998), (3) Frank and Groffman (1998), (4) Fisher and others (1982), (5) Frank and others (1998), (6) Scholes and others (2003), (7) Williams and Tonnesson (2000), (8) Nanus and others (2003), (9) Rundel and others (1982), (10) Tracy and Frank (1998), (11) Fisher (2006), (12) Schade and Hobbie (2005), (13) Peterjohn and Schlesinger (1991), (14) Holmes and others (1996), (15) van Wilgen and others (2003), (16) Naiman and others (2003).

¹⁷ Note that the figures for nitrogen mineralization are not directly comparable across semiarid African, semiarid North America and temperate North America ecosystems as different techniques were used: Scholes and others (2003) and Fisher (2006) used an in situ technique for net nitrogen mineralization (metal tubes), Schade and Hobbie (2005) used a laboratory technique for potential nitrogen mineralization, whereas Frank and Groffman (1998) used the buried bag technique for net nitrogen mineralization.

Spatial heterogeneity in nutrient stocks and cycling exists at various scales in arid and semiarid uplands (for example, Schlesinger and others 1996), and is influential in conservation and export of terrestrially derived nutrients to riparian zones (Tongway and Ludwig 1997; Ludwig and others 2005). For example, fertile and infertile patches in southern African savannas correlate with spatial distribution of geologic and edaphic factors (Scholes and others 2003; Venter and others 2003). At a regional level, geology determines nutrient poor and rich patches, with nutrient poor soils encountered on granites and nutrient rich soils on basalt (Scholes and others 2003; Venter and others 2003). Within individual catchments, the functioning of smaller patches is partially controlled by their landscape position, with the sandy soils of crests being nutrient poor and the clayey soils of the mid- and lower slopes being richer in nitrogen

and phosphorus (Scholes and Walker 1993). Vegetation composition and patterning also reflect landscape position, with fine leaved leguminous woody species in the mid- and lower slopes and broadleaf vegetation in the crests (Figure 2). At smaller scales, individual vegetated patches are enriched in nutrients, organic material and fine material—and inter-vegetation (bare or sparsely vegetated areas) patches are often poor in nutrients (Georgiadis 1989; Figure 2). These generalizations for African savannas are consistent with findings from North American (Schlesinger and others 1990, 1996; Belnap and others 2005) and Australian semiarid and arid ecosystems (Tongway and Ludwig 1997). This spatial organization of vegetation and nutrient resources is influential in controlling export of nutrients to riparian zones (Tongway and Ludwig 1997) and thence, streams (Wiens 2002).



Figure 2. Vegetative patches at various scales in nutrient poor semiarid southern African savannas. The photo on the top is an oblique aerial photo of a toposequence where (A) denotes the upland, (B) the midslope, in this case a broad sodic zone and (C) the riparian ecotone (Photo: courtesy of H. Eckardt, Kruger National Park). Broadleaf vegetation is associated with the uplands, fine leaved vegetation with the midslope and evergreen broadleaved vegetation with the riparian zone. The lower photo shows vegetative (A) and intervegetation patches (B) in a sodic zone, which is frequented by ungulate grazers.

Water is the primary control over nitrogen and phosphorus cycling in semiarid and arid regions of the world, regardless of local soil fertility (Noy-Meir 1973; Scholes and Walker 1993). Water availability in semiarid African savanna environments is variable in both time and space (Tooth 2000; Venter and others 2003). Precipitation falls in discrete events, with varying intensity and duration, and is usually confined to a distinct wet season. A rainfall event breaking an extended dry period is usually followed by a sharp increase in net nitrogen mineralization (Scholes and others 2003). In the Sonoran Desert of North America, Welter and others (2005) found that ammonium accumulated during dry periods but was rapidly depleted through nitrification when rains occurred, similar to African

savannas (Scholes and others 2003). Nitrogen pools in fine-textured soils tend to be larger than in coarse-textured soils, for example in basalt soils in southern African savanna, resulting in a larger response of soil nitrogen mineralization to precipitation events than in a coarse-textured soil (<0.5 compared to $>2 \mu\text{g N g}^{-1}$ soil day; Scholes and others 2003). However, in riparian soils the amplitude of the biological response is likely smaller as the soil is often moist throughout most of the year, similar to tendencies found in more mesic environments (Hart and Firestone 1991; Belnap and others 2005). Whether repeated wet-dry cycles in semiarid uplands result in larger net effects than for continuously wet soils is much debated; however Austin and others (2004) summarized several studies that support this tendency. Soil available phosphorus also increases following drying-rewetting cycles, possibly due to the release of organic phosphorus from microbial biomass during dry periods (Turner and Haygarth 2001).

In African savannas, with deciduous woody vegetation and moribund grass after a dry season, a lag is often observed between the onset of summer rains and peak plant productivity (Augustine and McNaughton 2004). This asynchrony between nitrogen and phosphorus availability and peak plant productivity may represent a window when relatively high inorganic and organic nitrogen, phosphorus and sediment loads are exported to riparian zones and streams (see also Austin and others 2004). Relatively low potential for available nitrogen uptake by plants during the onset of summer rains may also provide an opportunity for trace nitrogen gas losses that help maintain nitrogen-limited conditions in savanna uplands (Davidson and others 1993; Scholes and others 1997; Otter and others 1999). Nitric acid emission rates, a major output pathway from African semiarid savannas, are often highest at the start of the rainy season (Otter and others 1999).

Delivery of Nutrients to the Riparian Zone

Even small precipitation events trigger the redistribution of sediment, nutrients and organic material from upslope positions in savannas. However, large material fluxes follow high intensity and/or high frequency events (Wilcox and others 2003; Loik and others 2004). Soils in semiarid environments typically have low infiltration capacity, and juxtaposed with low interception losses and high intensity of rainfall events, this results in significant overland flow during precipitation (Dunne and

Leopold 1978; Fisher and others 1998; Tooth 2000; Belnap and others 2005; Figure 1). Numerous studies in semiarid regions show that most runoff and sediment movement is generated from bare patches where infiltration capacity is low, and little runoff is generated from areas covered with trees or shrubs, and less still comes from grassy areas (Wilcox and others 1997; Reid and others 1999). Additionally, biological soil crusts, consisting of mosses, lichens, algae and blue-green algae cover bare soil in many semiarid areas of the world and act to reduce infiltration (Belnap and others 2005). Biological crusts have been shown to fix nitrogen, but crust integrity is compromised by hoof action from large herbivores. Runoff then transports nitrogen-rich crust fragments downslope until captured in a vegetated patch.

Runoff thus contains both particulate and dissolved inorganic and organic nitrogen and phosphorus. At the start of the rainy season this organic and inorganic nitrogen and phosphorus may originate from accumulation during the dry season, atmospheric dry deposition and deposition in animal waste (Figure 1; Table 1), the latter two processes being particularly important in South African savannas (Scholes and others 2003; Augustine and McNaughton 2004). Trampling by large animals is also a significant disturbance of the soil surface; the resultant sediment loads may contribute significantly to downslope transport of nutrients. Winter fires represent a major output vector of nitrogen from savanna uplands via the process of volatilization, but they also deposit nutrient rich ash on the soil surface. In North American deserts Schlesinger and others (1999) recorded small but significant amounts of dissolved inorganic and organic nitrogen and phosphorus in surface runoff from inter-vegetation patches in a semiarid catchment. Even though vegetated patches produced less runoff, nutrient concentrations were much higher, commensurate with the finding of Ludwig and Tongway (1997) that vegetated patches in Australian savannas are often enriched in nutrients. When coupled with the dramatic changes in soil microbial processing initiated by rainfall, total nutrient transport by overland flows as well as the form of nutrients transported is strongly responsive to temporal distribution of storms (for example, Welter and others 2005). Fierer and Gabet (2002) found that raindrops, through mobilization of soil particles from the topsoil during impact, increase transport of mineral nitrogen and carbon as well as organic nitrogen over that measured in runoff alone. Evidence from African savanna ecosystems is lacking, however;

the preponderance of overland flow contrasts with mesic environments, which often have higher plant cover, thicker litter layers and higher infiltration rates, resulting in vertical rather than lateral movement of water and associated nutrients.

Herbivore activities can significantly enhance surface runoff generation—and sediment and nutrient transport—by changing the structure and biogeochemical characteristics of patches and boundaries (Ludwig and Tongway 1997). African savannas contain high numbers and a high diversity of herbivores and carnivores (du Toit 2003). Well-defined game paths created by herbivores such as hippopotamus (*Hippopotamus amphibius*) often cross the upland-riparian boundary and provide a measure of connectivity between patches (Naiman and Rogers 1997; Naiman and others 2003). Soils within game paths are typically enriched in dung and urine which contain large amounts of nitrogen and phosphorus (Grant and others 2000), similar to other areas where game congregates, such as around waterpoints (du Toit and others 1990). These soils are often compacted, reducing infiltration capacity and increasing focused, overland transport of material between patches (Puth and Wilson 2001; Pickett and others 2003). Game paths leading from riparian zones to streams can deliver sediment and nutrients directly to streams, short circuiting the capture and retention mechanisms associated with riparian zones. Increased herbivore activity within riparian zones also may make the biotic transfer vector for nutrients especially important during the dry season, when hydrologic delivery of nutrients essentially shuts down (Figure 1). The role of herbivores as lateral vectors in riparian biogeochemistry of African savannas is an area ripe for further investigation, because it contrasts strongly with the situation in many other semiarid and arid—and some mesic—regions of the world.

Fire is an integral ecosystem driver in savannas and grassland. Fire also leads to more runoff and erosion by reducing vegetation cover (Beeson and others 2001; Johansen and others 2001) and reducing patch integrity (Ludwig and others 2005). Depending on soil characteristics, fire can also decrease soil wettability, thus increasing entrainment of sediment (Shakesby and others 2000). This changes upland areas from resource (water, nutrients) conserving to “leaky” landscapes, thus allowing nutrients to be delivered to the riparian zone. When fires occur before or during the wet season, ash and soil containing nitrogen, phosphorus and cations are mobilized in the uplands during subsequent rainstorms and deposited

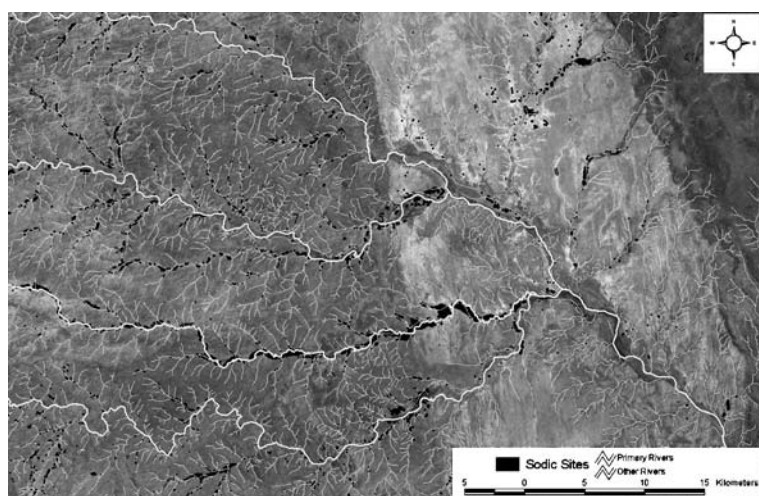


Figure 3. Distribution of sodic soils in the semiarid Lowveld savanna in northeast South Africa. Sodic patches were identified using Landsat imagery and unsupervised classification, and are indicated by *dark areas* that follow river courses. The effect of geology on vegetation structure can be clearly distinguished, with basalts occupying the *lighter colored* eastern sections (high grass biomass) and granites the *darker* western areas (more wooded communities). (Photo: courtesy of Sandra McFadyen, Kruger National Park).

downslope (Townsend and Douglas 2000). Fire also enhances mineralization of nitrogen and phosphorus in upland soils (Frost and Robertson 1987; Wan and others 2001). In more mesic environments, fire, though occurring less regularly (Table 1), has been correlated with elevated concentrations of dissolved nutrients in stream ecosystems (Minshall and others 1989). In African savannas runoff from bare patches is also enhanced through formation of physical soil crusts, the formation of which is enhanced by fire (Mills and Fey 2004). Mills and Fey (2003) noted that raindrops falling between vegetated patches also encourage the formation of physical soil crusts by collapsing aggregates and dispersing clay particles at the soil surface; this, in turn, encourages the formation of biological soil crusts. Both fire and crust formation (physical and biological) seems to be less important in mesic environments (Table 1; Belnap and Lange 2003).

Sodic Patches as a Source and Sink for Nutrients

The linkage between uplands and riparian zones is strongly dependent on patch characteristics, which enhance or diminish the flow of material (Tongway and Ludwig 1997; Pickett and others 2003). Perhaps unique to arid and semiarid regions, salts accumulate near the soil surface at predictable points along hydrologic pathways, giving rise to saline or sodic patches. Sodic soils tend to form along the upland edge of riparian zones in the African savanna (Khomu and Rogers 2005; Figures 2, 3) and elsewhere (Tóth and others 2001) where groundwater seeps emerge near the base of hillslopes or where trees have access to saline

ground water (Abrol and others 1988; Sophocleous 2002). Although there has been little study of the effects of sodic soils on riparian ecology, alterations to the physical, chemical and biological environment caused by sodication have predictable implications for transfers of materials across riparian boundaries.

Perhaps the most important influence of sodic soils stems from alteration of hydrologic pathways across the upland-riparian boundary, affecting transfers of water, nutrients and soil particles. Clay dispersion in sodic soils causes soil surface crusting and loss of soil structure (Chappel 1992; Qadir and Schubert 2002). Infiltration and hydraulic conductivity are further limited by soil swelling. As a consequence, fluxes of shallow subsurface water are more restricted than in non-sodic areas of similar landscape position (Abrol and others 1988). In addition, dispersed soils are susceptible to gully erosion, focusing the movement of water, sediment and nutrients across the riparian boundary and thus limiting opportunities for infiltration into riparian soils (Chappel 1992; Qadir and Schubert 2002). Although low porosity reduces fluxes of water through sodic soils, clay dispersion increases the mobility of clays and organic matter that is desorbed or released from dispersed aggregates (Nelson and others 1998). Mobilized clay and organic matter either move down through the soil profile forming an impervious natric horizon further restricting infiltration or are drawn up to the soil surface through capillary movement. In either case, substantial amounts of clay are redistributed to down slope areas over time (Huggett 1976).

As water moves through sodic soils, gaseous losses of nitrogen may prevent N-movement from uplands into riparian zones. Waterlogging of dis-

persed sodic soils creates conditions favorable for denitrification and other redox-driven reactions. Denitrification is further favored by large pools of soluble organic matter in sodic tree-grass systems (for example, Kaur and others 2002), because denitrification is frequently carbon-limited (Pinay and others 1993; Naiman and Décamps 1997). Fisher (2006) found relatively high rates of denitrification enzyme activity in sodic soils, second only to the nearby savanna riparian area (ranging from 2.0 to 10.0 $\mu\text{g N (N}_2\text{O) kg}^{-1} \text{ h}^{-1}$ in the sodic area to 4.0–33.0 $\mu\text{g N (N}_2\text{O) kg}^{-1} \text{ h}^{-1}$ in the riparian zone). Although ammonia emissions are often considered a minor flux in natural soils (Schlesinger and Hartley 1992), ecologically significant soil losses may result from the high alkalinity typical of sodic soils, which favors formation of ammonia over non-volatile ammonium. Substantial volatilization may also originate from ammonia in dung and urine deposited by large herbivores foraging on sodic areas, which frequently have soil pH values in excess of 7.5 (Dye and Walker 1980). Similarly, release of phosphate following reduction of iron and aluminum oxides in waterlogged soils (Richardson 1985) and preferential formation of soluble sodium phosphates over less soluble calcium phosphates at very high pH both can result in downslope translocations of soil phosphorus over time (Bertrand and others 2003). Sediment delivery downslope from sodic areas may be enhanced by the activities of large herbivores, which congregate on sodic patches to take advantage of seasonally nutritious forage and relative safety from predators. Sodic patches may thus be both a source of nitrogen and phosphorus to riparian areas, but may also attenuate fluxes to riparian areas through biotic sinks such as denitrification.

Biotic Nutrient Vectors

African savanna riparian zones are used extensively by large herbivores and carnivores, which act as ecosystem engineers by modifying the physical environment (Naiman and Rogers 1997) and transferring nutrients in feces and urine (Naiman and others 2003, 2005b). Biotic agents of nutrient flux are often underappreciated, yet large and small animals may in some cases contribute substantially to overall riparian nutrient budgets (for example, Post and others 1998; Helfield and Naiman 2006). These biotic subsidies can be strongly bi-directional, with transfers in either direction between land and water across riparian boundaries (Ballinger and Lake 2006). Spatial variation in biotic fluxes may

result from foraging and migration patterns operating at diel, seasonal, and interannual time scales.

Nutrient transfers by domesticated herbivores (for example, cattle) are well acknowledged as an important process in managed ecosystems (Belsky and others 1999). Riparian nutrient transfers by herbivores in natural settings have received far less empirical attention but are important as well. Fluxes may occur by many vectors. Herbivores residing primarily in upslope areas, yet which feed or drink in riparian corridors, may carry nutrients toward riparian zones. Similarly, herbivores residing primarily in water, yet which feed on terrestrial riparian vegetation, can transfer nutrients directly from land to water by physically moving vegetation or by excreting nutrients derived from terrestrial plant matter directly into water bodies (for example, many waterfowl, hippopotamus) (Post and others 1998; Lewison and Carter 2004). Many large and small animals also use riparian zones as longitudinal corridors, spending significant amounts of time within the confines of the riparian forest (Ballinger and Lake 2006). In semiarid areas birds concentrate in riparian areas, and can contribute significantly to riparian nutrient budgets (Naiman and others 2003; Post and others 1998). Herbivores may also indirectly affect riparian nutrient transfers by altering the physical structure of vegetation and its capacity to mediate nutrient transfers between the atmosphere, plants, and soils.

The impact of herbivores on riparian nutrient fluxes may be especially important in semiarid ecosystems where they are abundant, such as the southern African savannas. Water is an important factor controlling herbivore distributions, owing to its influence on the availability of quality forage and water for drinking. This is well illustrated by nitrogen and phosphorus concentration around artificial water holes in semiarid savanna (du Toit and others 1990). Animal dung and urine deposited by large herbivores concentrating around water holes enrich the soil and vegetation. Large herbivores, ranging from warthog to elephant also create biogeochemical hotspots through trampling and uprooting of vegetation (Naiman and Rogers 1997). On the corollary, large animals such as hippopotami can consume as much as approximately 135 kg riparian grasses daily, transferring large amounts of nutrients to the aquatic environments (Naiman and others 2005b). Similarly, large herbivores concentrate in riparian areas during the dry season (Gaylard and others 2003), depositing dung and urine, which may contribute substantially to nutrient flux at a time when low water runoff limits fluxes by hydrologic vectors. The

movement of herbivores to riparian areas during dry periods also concentrates and promotes carnivory (du Toit and others 2003), which may further increase biotic nutrient transfers.

LONGITUDINAL DELIVERY OF NUTRIENTS

Longitudinal hydrologic connectivity is critical for downstream nutrient transport, both for instream nutrient processing and for delivery of nutrients to the riparian system. Terrestrially derived nitrogen is augmented by fixation of atmospheric nitrogen by instream components such as cyanobacteria (Grimm and Petrone 1997; Dodds and others 2004) or riparian higher plants in symbiosis with *Rhizobium* (Fisher and others 2004; Jacobs and others 2007), which represent sources of new nitrogen to streams and riparian zones. However, much of the nitrogen entering headwater streams is removed instream by denitrification in hyporheic sediments or assimilated by biotic uptake, usually within short distances (Peterson and others 2001; Mulholland and others 2002). The few measurements of uptake length for semiarid streams conform to this generalization (Marti and others 1997; Mulholland and others 2002; Grimm and others 2005). Extensive exchange between surface and subsurface waters, including shallow riparian groundwater, presents additional opportunities for nitrogen removal (Holmes and others 1996; Schade and others 2001, 2005). Phosphorus processing has been less well studied in semiarid streams, but abiotic removal processes, such as adsorption or precipitation, may be significant.

Dent and others (2001) found that both nitrogen and phosphorus concentrations varied longitudinally in predictable patterns that reflected the distribution of surface–subsurface exchange sites and intervening biotic or abiotic processing. However, nutrient exchanges with hyporheic sediments and groundwater are highly dependent on channel morphology (Ward and others 2002; Fisher and others 2004). In reaches where bedrock dominates, such as encountered in some African savanna streams (Rountree and others 2000), longitudinal, vertical and lateral exchange between surface and subsurface zones—and biological activity at the interface—are limited. The picture that emerges is one of complex sequences of nutrient processing patches in both the stream and the riparian zone that are hydrologically linked both during low- and high-flow periods.

Seasonal low flows isolate river sections and disrupt longitudinal hydrologic connectivity in semiarid environments (Fisher and others 1998),

perhaps leading to concentration of particulate and dissolved nutrients in river pools and sediments. Terrestrial sediment and nutrients washed into streams by the first rains mix with nutrients in the river and may be washed downstream or transported into riparian areas by seasonal floods (Welter and others 2005). Nitrogen concentrations in flood-water are highest during events following long droughts, and concentrations decline with subsequent events (Marti and others 1997). Particulate and dissolved nitrogen and phosphorus reenter riparian zones during annual and intermittent floods, and in subsurface hydrologic flows, both at base flow and during floods. Little empirical data on longitudinal movement of nitrogen and phosphorus are available on African semiarid savannas compared to other ecosystems, examples of which are the arid Sycamore Creek ecosystem (Grimm and Petrone 1997) and the temperate Hubbard Brook ecosystem (Likens and Bormann 1995). However, it is clear that some major differences exist in longitudinal nutrient delivery between arid and temperate ecosystems. In many arid and semiarid ecosystems relatively low biomass in the uplands, large inter-vegetation spaces and the tendency of soils to form physical and biological soil crusts result in a steep rising limb on the hydrograph and high peak flow values during intense summer storms (Tooth 2000; Naiman and others 2005b; Camporeale and others 2006). In the semiarid African savanna riparian vegetation acts as nodes where sediment and nutrients are captured, thus increasing riparian nitrogen and phosphorus stocks. Similarly, sandbars and sediment in the macrochannel floor are habitat for reeds, forbs and trees, which capture and retain fine sediments and associated nutrients (Kotschy and others 2000).

Nutrients are also redistributed within the floodplain when vegetation is uprooted during floods, and deposited as woody piles downstream where nutrients are released over time (Pettit and Naiman 2005). Large infrequent floods (return interval of more than 75 years), exceeding normal wet season base flows by more than an order of magnitude, result in a resetting of geomorphic and biotic templates (Heritage and others 2001; Parsons and others 2005). This contrasts with afforested mesic systems where slower release of water from the uplands results in a relatively slow rising limb. Nevertheless, the occasional powerful flood, with a shorter return interval than those in semiarid ecosystems can result in equally dynamic changes (Naiman and others 2005b). Much uncertainty remains regarding the effect of sea-

sonal and intermittent variation in water levels in semiarid rivers on sink—source relationships between surface water and riparian sediments and vegetation.

ATMOSPHERIC DELIVERY OF NUTRIENTS

Nitrogen and phosphorus are delivered to riparian environments through atmospheric deposition directly to riparian vegetation or indirectly through deposition in the uplands (Figure 1). Nitrogen derived from biomass burning and fossil fuel consumption is returned to the landscape in the form of dry and wet deposition (Scholes and others 2003). In the southern African Lowveld, total nitrogen deposition rates are unusually large, exceeding $21 \text{ kg ha}^{-1} \text{ y}^{-1}$ (Scholes and others 2003; Table 1), with much of this derived from anthropogenic sources and the remainder from regional biomass burning. In other semiarid ecosystems lower rates of nitrogen deposition have been measured; however, this is increasing due to human perturbation of the nitrogen cycle (Asner and others 2001; Fenn and others 2003; Galloway and others 2003). A significant proportion of total nitrogen deposition is in the form of dissolved organic nitrogen (Neff and others 2003), a form of nitrogen that is less likely to be retained in upland and riparian vegetation (Caraco and Cole 2001; Perakis and Hedin 2002). Phosphorus inputs from atmospheric dust are known to be a significant contributor to ecosystem functioning in savanna ecosystems, for example, in the Okavango delta, where up to $0.13 \text{ kg P ha}^{-1} \text{ y}^{-1}$ is deposited annually from atmospheric dust (Garstang and others 1998).

Nitrogen and phosphorus deposition is also concentrated in riparian areas as riparian vegetation, by virtue of higher biomass and stature than the surrounding terrestrial vegetation, intercepts more nutrients in through fall and dry deposition than the surrounding vegetation (Tabacchi and others 2000). Riparian vegetation in semiarid environments, particularly in African savannas, consists of many evergreen species, whereas uplands are frequently deciduous. This increases the rate of dry deposition to riparian soils during the dry season when upland vegetation has shed its leaves. Furthermore, forest edges have been shown to be exceedingly efficient at capturing and concentrating nutrients suspended in air, either as dry or wet deposition (Weathers and others 2001). We suspect that well developed gallery forests in savannas should be efficient at trapping and concentrating atmospheric nutrients

because their tall stature compared to the uplands acts as a forest edge. The tall stature and large leaf area also increase stemfall and throughfall correspondingly.

PROCESSING OF NUTRIENTS IN THE RIPARIAN ZONE

Elevated water availability and easier access to soil nutrients increase productivity and biomass of riparian communities above that of adjacent upland communities in semiarid ecosystems (February and others 2006; Jacobs and Naiman 2007). That contrasts with some mesic regions where riparian productivity equals upland productivity, especially where both communities support woody vegetation, although this depends on plant succession within the riparian zone (Megonigal and others 1997; Balian and Naiman 2005). In southern Africa, semiarid riparian zones contain a large fraction of evergreen and some semi-deciduous trees, whereas deciduous and herbaceous vegetation exhibit lengthened phenology compared to upland areas (du Toit and others 2003). Savanna riparian zones often contain a discontinuous grassy understory, or patches of tall or short grass (Naiman and Rogers 1997; Jacobs and Naiman 2007), which form a physical buffer to trap sediment, water and nutrients. Grassy riparian zones have been shown to be highly effective in trapping suspended sediment in overland flow, with coarse particles being deposited first whereas smaller, more nutrient rich smaller particles are transported further into the riparian forest (Naiman and Décamps 1997; Naiman and others 2005b). Higher woody biomass in riparian zones, coupled with lengthened phenology suggests that a large fraction of nutrients transported in surface and subsurface runoff can be taken up and retained. This increases biomass and groundcover, thus increasing the ability of the understory to trap nutrients and sediments (Ludwig and others 2005). Savanna riparian vegetation, therefore, acts as a sink for essential nutrients, especially early in the season when upland productivity is still sub-optimal, and sediment and nutrients are transported downslope during storms. Nutrient uptake is balanced by the continual removal of vegetation by flooding and channel migration (for example, Parsons and others 2005), and by removal of green biomass and transport to other parts of the ecosystem by large and small herbivores (Naiman and Rogers 1997). However, where net uptake takes place, whether at seasonal or longer-time time scales, assimilated nutrients are locked up in

the green and woody biomass for long periods, only becoming available again when leaves, frass, twigs and roots are shed, usually during the dry season.

A large fraction of nutrients taken up in plants during the growing season are returned to the soil via litterfall and root turnover, where decomposition allows nutrients to become available for reuse by plants and microbes, or are lost from the soil (Naiman and others 2005b). Herbivores feeding on riparian plants also increase decomposition when urine and feces are deposited on the ground. Small amounts of organic nitrogen and phosphorus sequestered by soil microbes also become available for mineralization when the relatively short-lived organisms die. Soil hydrologic conditions are important in controlling nitrogen, phosphorus and carbon mineralization; moist, aerobic soils, such as found in savanna riparian soils (Bechtold and Naiman 2006) ensure high rates of mineralization (Chapin and others 2002). Mineralization in riparian soils reaches a peak during the early wet season, and is perhaps elevated further around pulsed rainfall events (Fisher 2006). Variable hydromorphic conditions in riparian soils also ensure that inorganic phosphorus is alternatively released or immobilized by complexing with Fe ions under anaerobic and aerobic conditions, respectively (Naiman and Décamps 1997).

In African savanna ecosystems, denitrification may be important in topographic depressions where water and runoff accumulate, such as wetlands, with anaerobic soils and a ready source of labile carbon (Pinay and others 1993). Denitrification has also been shown to occur in soil microsites within alluvial soils (Pinay and others 1992). Although denitrification in the soil matrix is relatively low in savanna riparian zones ($4.0\text{--}33.0\ \mu\text{g N (N}_2\text{O) kg}^{-1}\text{ h}^{-1}$ in Kruger National Park as compared to $281\text{--}583\ \mu\text{g N (N}_2\text{O) kg}^{-1}\text{ h}^{-1}$ in Yellowstone National Park, Table 1), substantial gaseous losses of nitrogen may take place as water residence time increases (McClain and others 2003). Dissimilatory nitrogen reduction to ammonium could be a third mechanism of nitrogen retention in riparian soil. This process is microbially mediated, requiring reducing conditions and low labile carbon levels (Silver and others 2001). Despite the apparent importance of dissimilatory nitrate reduction in various ecosystems, little is known about the process, and the implications for riparian biogeochemistry in semiarid savannas are not known.

RIPARIAN BIOGEOCHEMISTRY AND DISTURBANCE

Frequent disturbances are a distinguishing feature of riparian zones worldwide and exert strong controls on riparian form and function (Naiman and Décamps 1997; Naiman and others 2005b). Disturbances impact biogeochemical cycles by altering stocks of nutrients, changing reaction process rates, and reorganizing biotic communities and physical substrates that regulate reactions. In arid and semiarid ecosystems, floods and extended droughts are undoubtedly the major agents for biogeochemical disturbance and reorganization. An extreme example of flood disturbance is recorded in the February 2000 flood along the Sabie River in South Africa (Heritage and others 2001). During that flood, coming at the end of an extended drought, river discharge was estimated at about $6,000\text{--}7,000\ \text{m}^3\text{ s}^{-1}$, more than an order of magnitude larger than the mean annual flood peak of $290\ \text{m}^3\text{ s}^{-1}$ and the largest flood in approximately 75 years. This flood dramatically changed the geomorphology and riparian vegetation of the river corridor. Trees were toppled and redistributed downstream, where they formed approximately 200,000 woodpiles within about 135 km of the Sabie River in Kruger National Park (KNP) (Pettit and others 2005). These piles of large wood are playing important roles in the redevelopment of vegetation communities and in the physical and biogeochemical processes linked to them (Pettit and Naiman 2006, 2007a; Pettit and others 2006).

Conversely, extended droughts in the southern African savanna lead to reduced hydrological connectivity, changes in vegetation dynamics and animal movements, all potentially impacting on biogeochemical dynamics in the riparian zone (Naiman and Rogers 1997; Naiman and others 2007). Long drought periods encourage terrestrial plant species, lacking the necessary adaptations and life history characteristics for life in the riparian zone, to now benefit from the drier, more “terrestrialized” riparian soils. For example, in African savanna riparian zones, the composition of the riparian zone may change from broadleaved species to nitrogen fixing species with consequences for riparian soil and plant nitrogen stocks (Naiman and others 2005b). Drought in the uplands forces large herbivores and carnivores to spend long periods in riparian zones, where their activities have major consequences for biogeochemical dynamics. Both floods and extended droughts act as fluvial disturbances, but are at the same time essential for

maintaining the vitality and ecological integrity of riparian communities (Naiman and others 2007).

Given the fundamental role of vegetation in driving, regulating, and maintaining biogeochemical reactions, disturbances to vegetation communities can be used as a proxy for changes in biogeochemical cycles. This is an important proxy given the ease of studying vegetation compared to biogeochemical parameters and the large number of vegetation studies compared to biogeochemical studies. The destruction of vegetation by large infrequent floods sets in motion a series of changes in biogeochemical cycling proceeding differentially across the mosaic of channel and riparian patch types. In the Sabie River, the event caused a sudden decrease in the proportion of live to dead biomass and an increase in the proportion of nutrient remineralization compared to plant uptake. Overall, one would expect flood events of this nature to result in a temporary net loss of nutrients from the channel/riparian system as biomass is washed away and as post-flood river flows carry away the soluble (that is, NO_3) products of enhanced remineralization.

An inverse form of anthropogenic disturbance to the natural long-term cycles of vegetation and biogeochemical dynamics in semiarid African riparian corridors is the damming of rivers and elimination of natural flood regimes (for example, Hughes 1990; O'Connor 2001). Dams and water abstraction upstream resemble extended droughts in that they reduce both high flows and riparian groundwater levels, which gives rise to major modifications of semiarid riparian plant communities (Hughes 1990; Stave and others 2005). Drier conditions allow terrestrial species to enter and flourish in the riparian zone (O'Connor 2001; Naiman and others 2005b). The loss of longitudinal, lateral and vertical hydrologic connectivity and associated erosion of riparian soils contributes to significant modification of biogeochemical cycles (Stave and others 2005; Naiman and others 2005b). The reduction in flood peaks leads to a reduction in sediment and nutrient delivery to riparian zones (Nilsson and Berggren 2000; Pinay and others 2002). It also changes the ratio between soil nitrogen mineralization and denitrification, while emaciation of surface waters reduce contact between water and sediment, thus reducing rates of nutrient processing (Pinay and others 2002). A flattening of the hydrograph can also lead to a reduction in spatial heterogeneity such as wood piles created by large floods, which is crucial to plant community succession and maintenance of vitality of riparian zones (Pettit and Naiman 2005, 2006; Parsons and others 2005).

Contrasting with most mesic ecosystems, fire is a common disturbance in African savannas and a defining factor controlling savanna structure and composition (Scholes and Walker 1993; Table 1). The role of fire in riparian ecology is somewhat different, however, because fire is less common in riparian zones due to the higher mean moisture content of the vegetation, thereby probably lowering the intensity, severity, and frequency of fire (Dwire and Kauffman 2003; Pettit and Naiman 2007b). In fact, riparian zones—populated with evergreen trees and shrubs—and rivers often act as fire breaks in savannas (Naiman and others 2005b). Most fire impacts on riparian biogeochemistry instead originate in the uplands and are transferred to riparian zones along hydrologic flow paths. Fire enhances runoff through reduction of vegetation cover and heterogeneity (Beeson and others 2001; Johansen and others 2001) and, in some cases, through decreasing soil wettability (Shakesby and others 2000). When large fires occur in the wet season, ash and soil containing nitrogen, phosphorus and cations are mobilized in the uplands during rainstorms and deposited in the lower slopes and riparian zones. When fires do burn riparian zones, impacts are similar to those in the uplands, with ashed nutrients lost to aquatic ecosystems during rainfall events (Pettit and Naiman 2007a, b).

Many of the world's surface and ground waters are degraded from nutrient pollution, frequently as a result of uplands disturbances. There is a direct and positive correlation between total net nitrogen inputs to landscapes and riverine nitrogen export (Howarth and others 1996; Aber and others 1998; Caraco and Cole 1999). Semiarid and arid ecosystems are being increasingly exposed to elevated nitrogen deposition (Asner and others 2001). Nitrogen deposition in excess of $21 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in the Lowveld savanna of South Africa (Scholes and others 2003; Table 1) is comparable to nitrogen deposition rates in central Europe and even exceeds deposition rates in most of the continental USA (Fenn and others 1998; Nanus and others 2003). Elevated nitrogen deposition leads to nitrogen saturation, a state where nitrogen availability exceeds ecosystem demands. Nitrogen saturation manifests as elevated levels of nitrate in streamwater and has been measured in tributaries of rivers flowing through the Lowveld savanna (Scholes and others 2003; Ndala and others 2006). However, within the Lowveld savanna ecosystem, most rivers seem not to reflect elevated nitrate levels, perhaps as a result of instream processing, similar to other semiarid ecosystems (Fisher and others 1998). In addition, increasing productivity and internal

nitrogen use in response to increasing nitrogen deposition is predicted for savanna and semiarid areas, given adequate water and other associated nutrients, thus potentially counteracting nitrogen saturation (Asner and others 2001). Chronic nitrogen saturation of these generally low-nutrient ecosystems, however, may increase the probability of nitrogen saturation, especially when phosphorus or other essential nutrients are at low levels (Fenn and others 1998). Increased nitrogen export may occur primarily during seasonal transitions or in concert with re-wetting events, particularly if deposited nitrogen accumulates in soils during periods when plant uptake is constrained physiologically or phenologically by low water availability. In this way, elevated nitrogen deposition has potential to amplify natural patterns of asynchrony in nitrogen cycling and export, leading to even greater transfer of nitrate to fluvial ecosystems. Well functioning riparian ecosystems are expected to be key in attenuating nitrogen through denitrification and plant uptake (Galloway and others 2003).

SUMMARY

Semiarid savanna riparian ecotones are increasingly threatened by landuse change and other anthropogenic disturbances; yet, there is only a rudimentary understanding of their biogeochemical linkages with the uplands and their role in trapping and processing of nitrogen, phosphorus and other nutrients. Fundamental differences exist in the landscape template, spatial vegetation patterns, moisture regimes and abiotic and biotic vectors that preclude the direct application of existing riparian models from temperate ecosystems to the African savannas. For example, spatial heterogeneity in the distribution of woody and herbaceous vegetation is important for conservation of nutrients in savanna uplands, especially where primary productivity is limited by environmental conditions (Table 2). Nutrient poor and rich patches in the uplands exist at various scales, which control spatial pattern of nutrient fluxes and delivery to riparian areas. Sodic zones, seemingly restricted in distribution to some semiarid areas are intriguing in that they are closely associated with riparian zones, yet their role in modifying nutrient fluxes has not been considered in great detail. Moisture regimes, typically highly variable and pulsed in savannas, are an important temporal control on nutrient cycling and export to the riparian zone. Moisture regimes, landscape configuration and plant phenology combine when early

summer storms, happening before full leaf flush, facilitate export of nitrogen and phosphorus to riparian zones in overland flow (Table 2). Herein semiarid savannas differ substantially from most mesic regions where spatial heterogeneity in resources, climatic variability and plant phenology are less influential in controlling the lateral movement nutrients from upland areas.

The differences between temperate and semiarid savannas are also evident in the occurrence and ecological consequences of large infrequent disturbances. In KNP, an extended drought was followed by a large flood event in 2000 that destroyed much of the riparian vegetation and redistributed nutrient stocks in plant biomass and sediment. During periods of extended drought, woody nitrogen fixers are able to enter the drier riparian zones, while, following the flood, piles of large wood became locations where carbon, nitrogen and phosphorus were concentrated. Modifiers such as fire and herbivores, ubiquitous in African savannas, are able to enhance certain processes such as nutrient cycling in uplands and riparian zones, and also contribute to material flux. Large animals visiting riparian zones create hotspots for nitrogen mineralization and denitrification and export nutrients from riparian zones to both terrestrial and aquatic environments. Fire may enter riparian zones after large floods when flammable material in the form of large woodpiles is readily available. The interaction between the savanna template, both in the uplands and in the riparian zone, and the effects of disturbances and modifiers on sink-source relationships and biogeochemical functioning in the riparian zone needs much elucidation.

Understanding relationships between ecological processes in savanna uplands, riparian biogeochemistry and aquatic ecology is increasingly important in the management of large natural and semi-natural areas, such as the KNP. The adaptive management approach followed recognizes the role of heterogeneity in ecosystem functioning, using thresholds of potential concern as an early warning system for management intervention (Venter and others 2007). Improved knowledge on controls on nutrient export from savanna uplands, retention in riparian zones and the effects of disturbance will be instrumental in adding more resolution to the early warning system as it pertains to protection of rivers against eutropication, and enhance the understanding of savanna ecosystem functioning as a whole. This is especially relevant given the widespread anthropogenic changes to the inherent spatial heterogeneity of many savanna landscapes, as well as riparian environments. Multi-disciplinary

Table 2. Summary of the Major Differences between Mesic and Semiarid Savanna Riparian Ecotones

Ecological properties	Mesic catchment	Semiarid savanna catchment
Moisture availability	Less variable, leading to more efficient nutrient cycling	More variable, giving rise to pulse-like patterns in nutrient availability
Nutrient distribution	Less variable	Highly heterogeneous at various scales, influencing nutrient delivery to riparian corridors
Upland vegetation configuration	High plant density, thick litter layer in uplands, vertical movement of water resulting in subsurface-dominated runoff. This maximizes opportunities for soil retention and transformation of carbon and nutrients	Open, non-vegetated spaces result in soil surface crusting and surface-dominated runoff; larger dendritic drainage networks. This results in limited opportunities for soil modification of runoff; faster, more intense hydrologic response to rain events
Distribution of riparian vegetation in catchment	Lower-order streams flanked by riparian communities that are able to intercept and trap sediment and nutrients from the uplands	Lower order streams sometimes devoid of flanking riparian vegetation so that sediment and nutrients often pass directly from uplands to aquatic environments during rainstorms
Riparian vegetation configuration	Patchy cover; more or less productive than uplands	More continuous cover where present; often more productive than uplands
Hill slope lateral transfers	Deep infiltration, slow lateral movement. High contributions to groundwater.	Shallow rapid lateral movement. Retention in soil/bedrock interface layers. Slow recharge to groundwater. Rapid overland flow and sediment movement during extreme events.
Longitudinal delivery	Hydrologically 'losing' streams less common	Hydrologically 'losing' streams common, especially during the dry season leading to reversal of water and nutrient movement from surface water to riparian sediments
Nutrient processing	Discontinuity between phenology of upland and riparian vegetation less common, resulting in less pulse-like nutrient delivery and retention in riparian vegetation	Enhanced phenology and evergreen vegetation in riparian areas contrasts with the uplands. This enhances early season nutrient delivery and retention in riparian vegetation

Major structural and functional differences are listed.

studies encompassing both natural savanna and savanna converted to other uses, such as agriculture, could be useful in understanding the mechanisms for nutrient retention, the magnitude of nutrient export from uplands, and the functionality of riparian zones throughout semiarid southern Africa. Enhanced understanding of the interactions between the physical template and abiotic and biotic drivers and modifiers of riparian biogeochemistry will be crucial in developing scientifically-based policies to prevent degradation of water quality in the fast-developing savanna region of Africa.

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